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BOTANICAL GAZETTE

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# ROOT SYSTEMS OF CERTAIN DESERT PLANTS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 236

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(WITH THIRTY-THREE FIGURES)

## Introduction

Although the aerial parts of plants have long been studied, little was known of the nature of the subterranean parts until the work of CANNON[1] upon the plants of the region about Tucson, Arizona. The supposition had been that in general the roots of desert plants are of great length and deep penetration. The work of CANNON showed that while this is sometimes true, such roots are often of no unusual length and in some cases are very superficial.

Since the soil conditions and the flora of the vicinity of Albuquerque are different from those at Tucson, a study of the roots of plants was undertaken in that vicinity, during the first half of the year 1915. Albuquerque lies in the valley of the Rio Grande, on each side of which are bluffs, leading to an apparently level upland. The mesa on the east rises from an elevation of 200–300 ft. above the valley floor to an elevation of 1200–1500 ft. at the base of the Sandia Mountains 10 miles farther east. This mesa is composed to a great depth entirely of unconsolidated materials, as is shown by a boring of the Water Supply Company 725 ft. deep.[2] It is

[1] CANNON, W. A., The root systems of desert plants. Publ. Carnegie Inst. Wash. no. 131.

[2] BRYAN, K., Geology of the vicinity of Albuquerque. Bull. Univ. N. Mex. no. 5.

concluded from this that previous to the deposition of these beds there was here a deep trough, which other evidence shows to have been the bed of a large river, which existed at a period of greater precipitation and was subsequently filled with stream-borne material. On account of its fluviatile origin the material is extremely variable, being composed of layers of sand, adobe, clay, gravel, boulders, and combinations of these materials, with marked local variations, both horizontally and vertically. On this mesa and the numerous arroyos which dissect its edge grew the plants studied.

One of the principal features of the soil in the habitats described by CANNON is a thick layer of hardpan, or *caliche*, beginning at a depth of about 30 cm. and extending indefinitely. This is so hard as to prevent root penetration, except through cracks. Such layers are common in arid regions, and are formed, according to the opinion of CANNON and others, through the concentration of salts left by the evaporation of ground water gradually ascending by capillarity. Rainfall dissolves these materials, carrying them downward. These two processes result in the formation of a gradually increasing zone of precipitation. In the Albuquerque region this zone is very poorly developed, often being noticeable in a fresh exposure only by the presence of a whitish streak or pebbles stained with lime. When dry, such soil becomes very hard, and it is evident from the appearance of roots entering it that it offers considerable resistance to root penetration, but does not prevent it. When wet the hardpan is soft and easily penetrable. Under natural conditions, however, it is generally very dry.

The Albuquerque region is even more arid than that at Tucson, an average for 10 years giving a precipitation of 7.44 in., as compared with an average of 11.17 for Tucson. Much of this small amount is lost by run-off, since most of the precipitation occurs as torrential summer rains. Table I shows the localization of the rains in the summer months. The marked deviations from the average that are characteristic of individual years are shown by the precipitation during the time of this study in 1915. The lower temperature and the smaller amount of precipitation in the winter

months prevent the growth of the winter annuals so characteristic of the Tucson region.

TABLE I

RAINFALL

| | Jan. | Feb. | Mar. | April | May | June | July | Aug. | Sept. | Oct. | Nov. | Dec. | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Tucson | 0.79 | 0.90 | 0.77 | 0.27 | 0.14 | 0.26 | 2.46 | 2.66 | 1.16 | 0.64 | 0.81 | 1.00 | 11.17 |
| Albuquerque, average | 0.48 | 0.33 | 0.22 | 0.26 | 0.69 | 0.35 | 1.43 | 1.07 | 1.70 | 0.77 | 0.46 | 31 | 7.44 |
| Albuquerque, 1915 | 0.68 | 0.56 | 0.51 | 2.05 | 0.00 | 0.00 | .... | .... | .... | .... | .... | .... | ..... |

TEMPERATURE

| | 1893 | 1894 | 1895 | 1896 | 1897 | 1898 | 1899 | 1900 | 1901 | 1902 |
|---|---|---|---|---|---|---|---|---|---|---|
| Absolute minimum | 11 | 0 | 10 | 13 | 2 | 0 | 1 | 9 | 4 | 12 |
| Absolute maximum | 98 | 95 | 95 | 100 | 95 | 104 | 104 | 101 | 99 | 100 |

EVAPORATION FROM A FREE WATER SURFACE

| Jan. | Feb. | March | April | May | June | July | August | Sept. | October | Nov. | Dec. |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 2.04 | 2.63 | 6.17 | 6.82 | 10.08 | 12.63 | 11.78 | 10.21 | 8.00 | 4.38 | 1.73 | 1.40 |

The data for Tucson are given by COVILLE and MACDOUGAL[3] and those for Albuquerque by MAGNUSSON.[4]

A series of determinations of soil moisture was begun, but it was soon found that such data are of little value, since on account of the fact that the soil is composed of stream-borne material, it is subject to extreme local variations, even within the habitat of a single plant, as is shown in the descriptions of the habitats of most of the plants given in this paper. Samples of soil from different levels in the habitat of *Atriplex canescens* showed the following variations in moisture content, the percentages being based upon the dry weight of the soil. Coarse gravel at a depth of 1 ft., 4 per cent; fine sand at 2.5 ft., 10 per cent; hardpan at 4 ft., 3 per cent. Since the precipitation during the time of this study was

[3] COVILLE, F. V., and MacDougal, D. T., Desert botanical laboratory of the Carnegie Institution. Publ. Carnegie Inst. Wash. no. 6.

[4] MAGNUSSON, C. E., Bull. Univ. N. Mex. no. 5.

several times, the normal amount, the figures would have had even less value than usual. Similar variations in water holding capacity and wilting coefficient would result from the lack of uniformity in the soil.

On account of climatic differences, the flora is very different from that of the Tucson region. The larger cacti are absent here, all being low forms, excepting *Opuntia arborescens*. No tree is found on the mesa or its arroyos, and the bushes, except *Chilopsis saligna*, are seldom more than 5 ft. in height. The period of greatest growth follows the rainy season, whenever it may occur. There are no winter annuals here, the corresponding forms being either biennials or summer annuals. The annual plants are greatly in the minority, the most conspicuous part of the flora being composed of perennial herbs.

The principal plant associations occurring within the area studied are as follows.

1. The *Bouteloua* association, characterized by the grama and other grasses and formerly occupying the entire mesa, but now much invaded by ruderals, such as *Gutierrezia Sarothrae* and *Salsola*.

2. The *Dysodia-Ephedra* association, dominated by *Ephedra trifurca* and *Dysodia acerosum*. The majority of the plants have reduced aerial parts and a large root system. The association occupies the top and the upper portion of the sides of the gravelly ridges between the arroyos, where exposure and run-off are maximum. The soil is often pure gravel and the surface is generally a mosaic of pebbles.

3. The *Chrysothamnus* association, dominated by *Chrysothamnus Bigelovii* and occupying the lower parts of the sides of the arroyos. The soil is generally adobe, often with much sand and gravel.

4. The *Fallugia* association, dominated by *Fallugia paradoxa* and forming a narrow fringe along the beds of arroyos, which are generally covered with loose sand and gravel.

## Method of work

Annuals, biennials, and some of the smaller perennials were removed from the ground and photographed. On account of the difficulty of obtaining the delicate ultimate parts of the roots,

many are necessarily incomplete. It was found possible to photograph some of the larger perennials *in situ*, but in general it was found much more satisfactory to make accurate diagrams of the horizontal and vertical extensions of the root systems on paper metrically ruled in squares. The diagrams appear here drawn to a scale of 1:20, except figs. 25 and 26. While in general only the roots lying in or near a particular plane are represented, it was generally found possible without much distortion to include the most important part of each root system in both the horizontal and vertical diagrams. Roots that for some reason were not followed to the end are terminated in the diagrams by a broken line. Roots turning to a direction at right angles to the plane of the diagram end in a dot.

CANNON divides root systems into 3 types: (1) a generalized type, in which there is a well balanced development of both tap and lateral roots; (2) a specialized form, in which the tap root is much the more prominent; and (3) a second specialized form, characterized by a relatively better development of the lateral roots. This classification is used in the present paper.

## Description of root sytems

### ANNUALS AND BIENNIALS

*Biscutella Wislizeni*.—This plant is common in sandy situations on the mesa and in the arroyos. The root system consists of a relatively short tap root, with many strongly developed laterals extending horizontally rather near the surface of the soil. Some of them usually exceed the tap root in length. The specimen shown in fig. 1 grew in a sandy arroyo bed and was about 10 in. in height.

*Phacelia corrugata*.—This plant is common in a number of associations. It generally occurs as an annual, although specimens in favorable situations may start in the fall and form rosettes which survive the winter. The leaf structure shows almost no xerophytic characteristics, there being only one layer of palisades, large air spaces, and a thin epidermal wall. Considerable variation of the root system occurs under different soil conditions. The plant

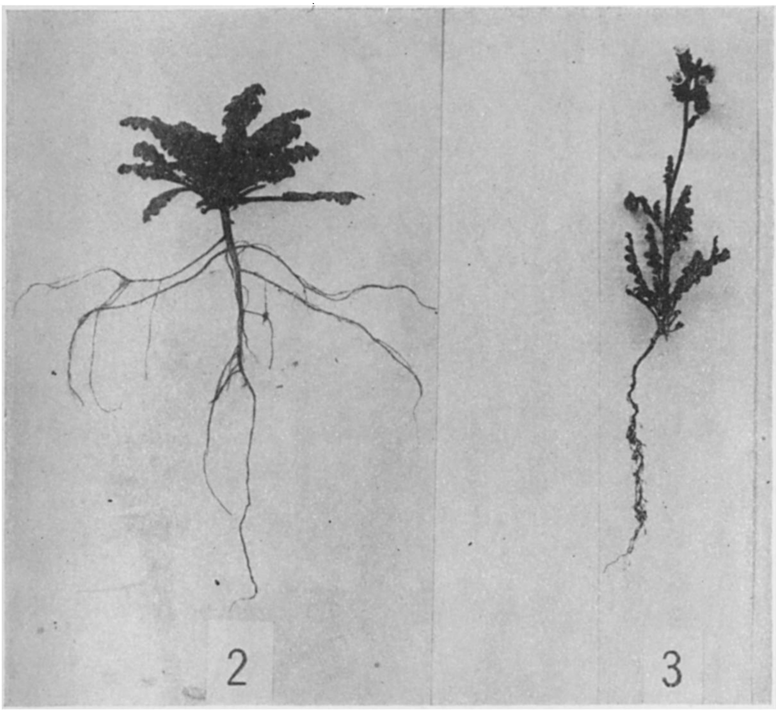
shown in fig. 2 grew in a moist situation, where the water of an arroyo was impounded by a dam. The plant is in its early spring condition, the rosette having survived the winter. The root system is of the generalized type. The laterals near the surface are especially well developed, sometimes exceeding the tap root in length. The specimen shown in fig. 3 is from a dry, gravelly ridge in the *Dysodia-Ephedra* association. The impoverished condition of the plant is shown by the weak development of both root and shoot. Here the tap root is relatively the more important.

FIG. 1.—*Biscutella Wislizeni*

*Allocarya crassisepala.*—This is one of the most common annuals of the mesa and arroyos and is a ruderal in a number of associations. The plants vary very greatly with the soil conditions in both root and shoot. The plant shown in fig. 4 grew in moist soil in the bottom of an arroyo and bore numerous prostrate branches. The root system was superficial and consisted of a short tap root which soon became horizontal, and a number of long, branched laterals arising about an inch below the surface of the soil. The plant shown in fig. 5 grew in dry soil and had a tap root relatively well developed and vertical, with smaller and less numerous laterals.

*Sisymbrium canescens.*—This plant is common in a number of associations. It makes a quick growth and maturity after a period of rain. The root system is very small in proportion to the shoot and consists of a tap root with a number of small laterals.

*Linum rigidum*.—This plant is characteristic of the *Dysodia-Ephedra* association. Both root and shoot are much reduced. The root system in the plant shown in fig. 7 consisted of a tap root about 5 in. long and a few short laterals with almost no fine ultimate branches.



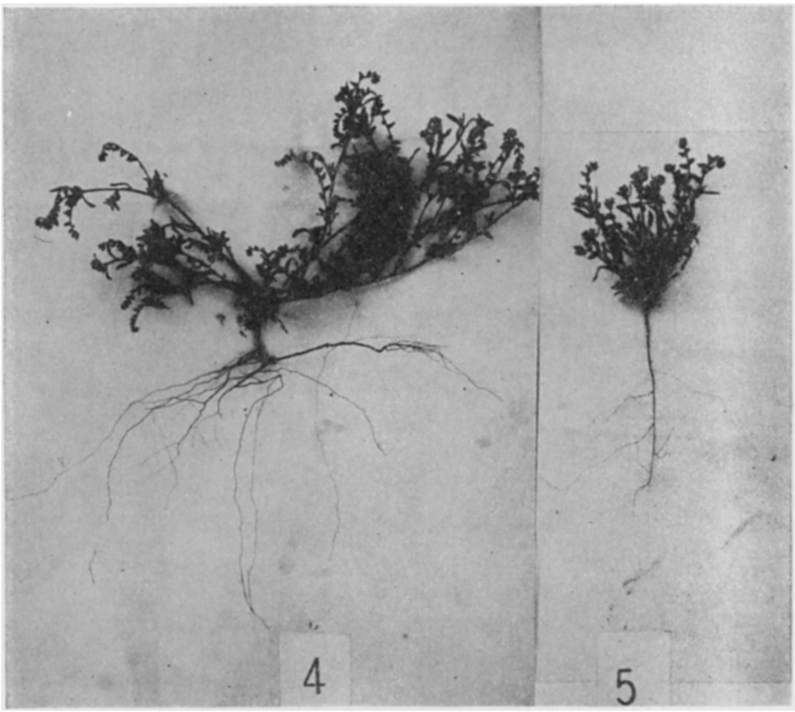

FIGS. 2, 3.—Fig. 2, *Phacelia corrugata* from moist habitat; fig. 3, *P. corrugata* from dry habitat.

PERENNIAL HERBS

*Cymopterus Fendleri*.—This plant is exceedingly common on the mesa and the ridges between the arroyos. It is the earliest plant to begin growth and to blossom in the spring. The leaves are in the form of a loose rosette and are xerophytic in structure. The root system is characterized by a thick, fleshy tap root which occasionally bears one or two fleshy laterals. In the growing season there appear numerous slender, white, absorptive roots

which later are deciduous. These always break off upon removal from the soil and do not appear in the figure.

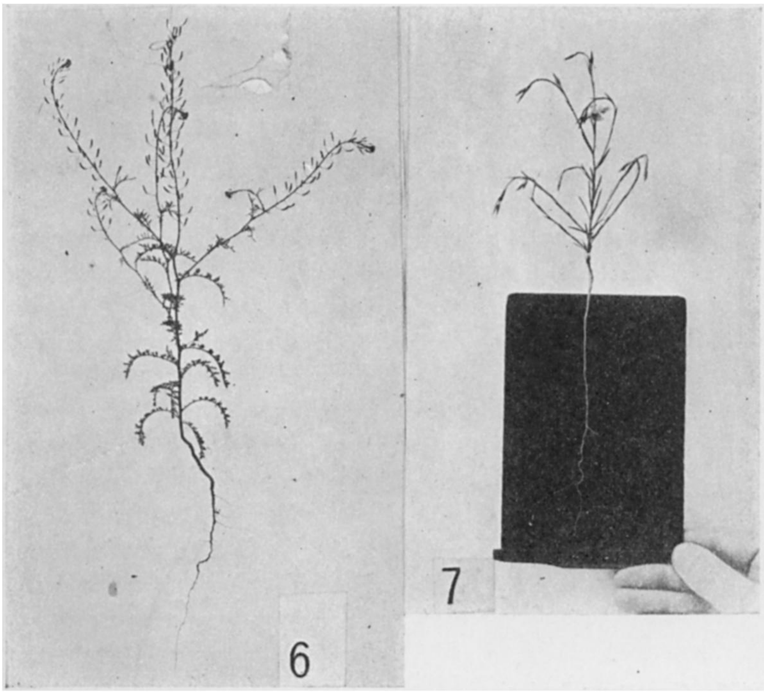
*Rumex hymenosepalus*.—This plant is common in the more mesophytic places on the mesa, especially in broad, shallow arroyos. The rosette of broad, thick leaves appears very early in the spring and is soon followed by a spike of flowers. The root is very large




FIGS. 4, 5.—Fig. 4, *Allocarya crassisepala* from moist habitat; fig. 5, *A. crassisepala* from dry habitat.

and fleshy. Young roots are constantly being formed as the oldest decay. The irregular projections at the top of the root shown in fig. 9 represent 10 or 11 crowns of former years. The youngest roots bear short laterals, but the older ones are generally without them. It is interesting to note that of the plants studied the three having the most prominent storage organs in the way of thickened roots all grow in situations more mesophytic than the average.

*Rumex* is common in the arroyos on the mesa; *Cucurbita foetidissima* occurs most abundantly along the banks of irrigation ditches in the valley; *Berlandiera lyrata* is confined almost entirely to the sides of arroyo beds. Thus it appears that the plants having this "adaptation" to an arid environment are in less need of it than most of the plants of the region.




FIGS. 6, 7.—Fig. 6, *Sisymbrium canescens;* fig. 7, *Linum rigidum*

*Astragalus diphysus* and *A. mollissimus*.—These are common evergreen plants of the mesa. The root systems are similar and are characterized by prominent tap roots with a few large and several small laterals, which are generally deeply placed. The root tubercles are small and not numerous. A plant of *A. mollissimus* is shown in fig. 10.

*Solanum eleagnifolium*.—This plant is very characteristic of sandy situations and the rapidly eroding sides of arroyos. The

plant shown in fig. 11 grew in the latter situation. The upper 12 in. of soil was sandy adobe, followed by 10 in. of clayey adobe with some gravel. Below this was a layer of loose gravel about 2 in. in thickness, under which was fine sand to an unknown depth. The plant was 18 in. in height. The root system was of the specialized type with strongly developed tap root. There were a few well developed laterals, two of which arose at the junction of the layers of sandy and clayey adobe. Upon reaching the layer of loose gravel, one of these turned abruptly and proceeded horizontally in the gravel layer, possibly on account of the greater ease of penetration. Another took a rather tortuous course downward and was lost at a depth of 65 in., below the level of the bottom of the arroyo. This root had a length of 72 in., and since its diameter at the broken end was 3 mm., its total length was undoubtedly much greater. Numerous small laterals arose in the upper 12 in. of soil.

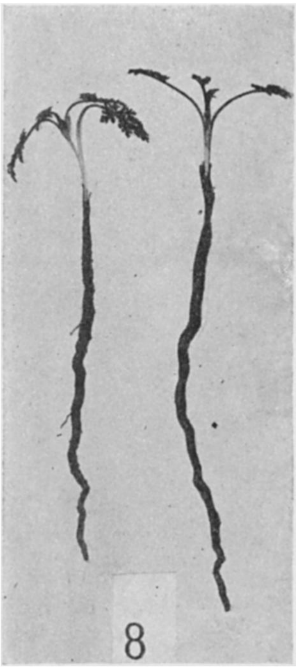


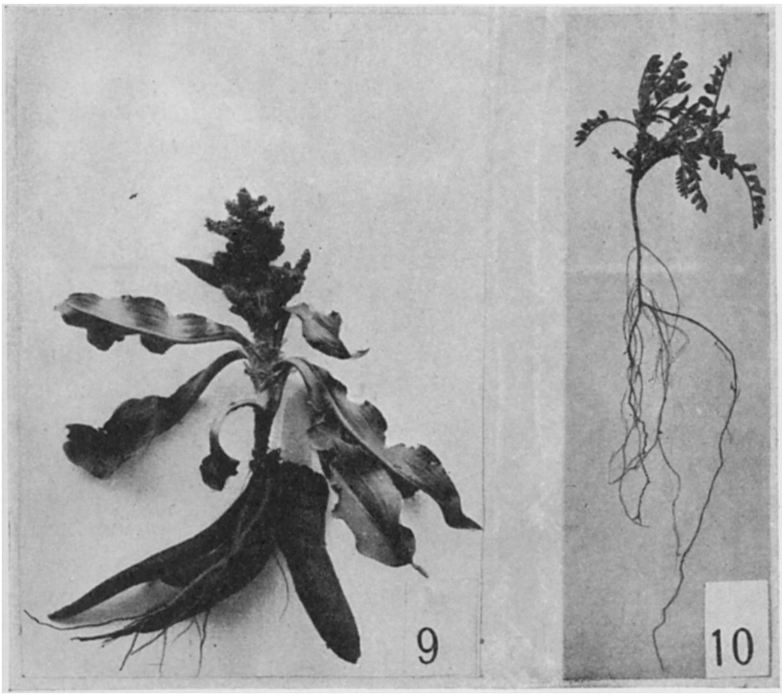

FIG. 8.—*Cymopterus Fendleri*

*Cucurbita foetidissima.*—This perennial herbaceous vine is common along irrigation ditches in the valley and less so along the sides of arroyo beds. The root is extremely thick and fleshy and is surmounted by an underground stem 6 in. in length. The main root of the plant studied was about 3.5 in. in diameter at the top and extended to a depth of 20 in., gradually becoming horizontal and forking several times after reaching a length of 36 in. The main root bore only one small lateral (fig. 12).

*Pachylophus hirsutus.*—This plant is a rosette in habit and is found in the driest and most exposed slopes of the gravelly ridges of the *Dysodia-Ephedra* association. The leaves are hairy and rather thick and succulent. The root system is fleshy and of

irregular form, without evident differentiation into tap root and laterals. The main root often proceeds horizontally and is little larger than the minor roots. The specimen shown in fig. 13 grew in pure gravel.

*Euphorbia* sp.—This small, prostrate plant grows on the sides of arroyo beds. The root system has much the same general form




FIGS. 9, 10.—Fig. 9, *Rumex hymenosepalus;* fig. 10, *Astragalus mollissimus*

as that of *Sphaeralcea*, but all the roots are slender, brown, and fibrous. The identity of the tap root is lost a short distance below the surface. The slender ultimate branches are very numerous. The root system is not deep, but very thoroughly permeates a limited amount of soil (fig. 14).

*Sphaeralcea cuspidata.*—This plant is very common in the *Bouteloua* and *Dysodia-Ephedra* associations. The plant shown in

fig. 15 grew in sandy soil on the mesa. The root system is characterized by a tap root which is poorly differentiated or even absent, and very prominent laterals. The remains of the crowns of several years are shown. When the plant grows in an unstable situation, such as the rapidly eroding side of an arroyo, vegetative reproduction from the roots occurs very commonly, enabling the plant to maintain a foothold.

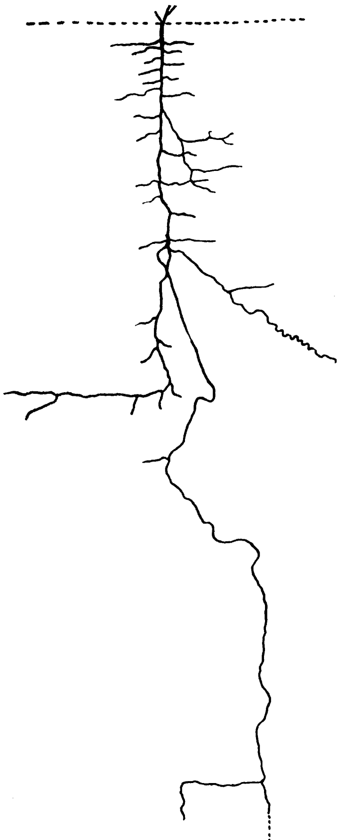
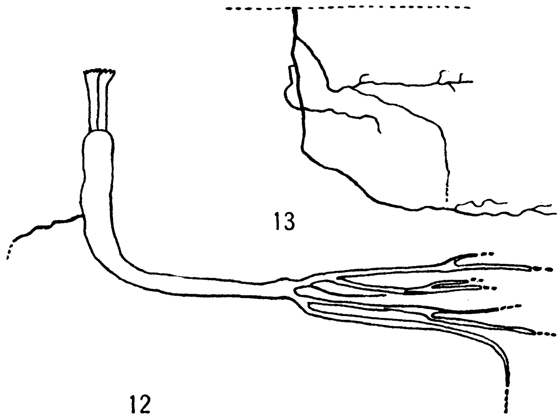


FIG. 11.—Vertical extension of root system of *Solanum eleagnifolium*.

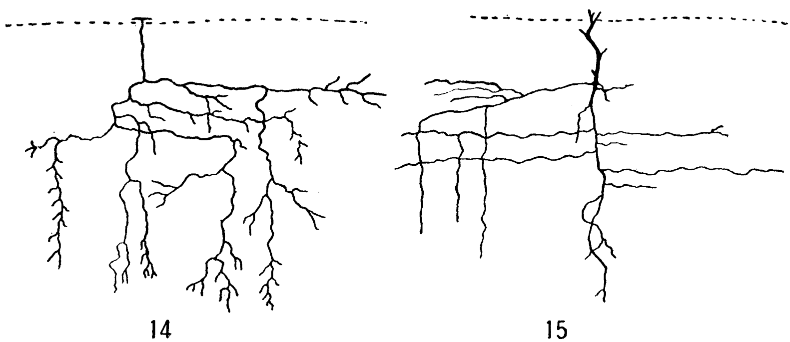
*Berlandiera lyrata*.—This plant is confined almost entirely to the sides of arroyo beds. The root system has a stout tap root with very few laterals. The group of laterals near the surface of the ground in so many plants of the region is absent here. The entire root system is thick and fleshy and the upper portion is swollen to the thickness of an inch. Plant *A*, fig. 16, grew about 1 ft. above the bed of an arroyo. The tap root divided into two horizontal branches slightly below the level of the arroyo bed. Plant *B* grew about 4 ft. above the bed of an arroyo and bore no extensive laterals until it reached the level of the bed of the arroyo, where it branched freely. The length of the tap root is apparently determined by the distance to the layer of moister soil on a level with the arroyo bed.

*Gaura coccinea*.—This perennial herb is very common on eroding arroyo sides and other disturbed situations. The root system belongs to the specialized type with prominent tap root. The length of the tap root is apparently determined by the distance of the plant above the arroyo bed. There are few laterals, most of

the absorption probably being done by the ultimate branches of the tap root. Vegetative reproduction from the roots is common (fig. 17).




FIGS. 12, 13.—Fig. 12, vertical extension of root system of *Cucurbita foetidissima;* fig. 13, vertical extension of root system of *Pachylophus hirsutus.*

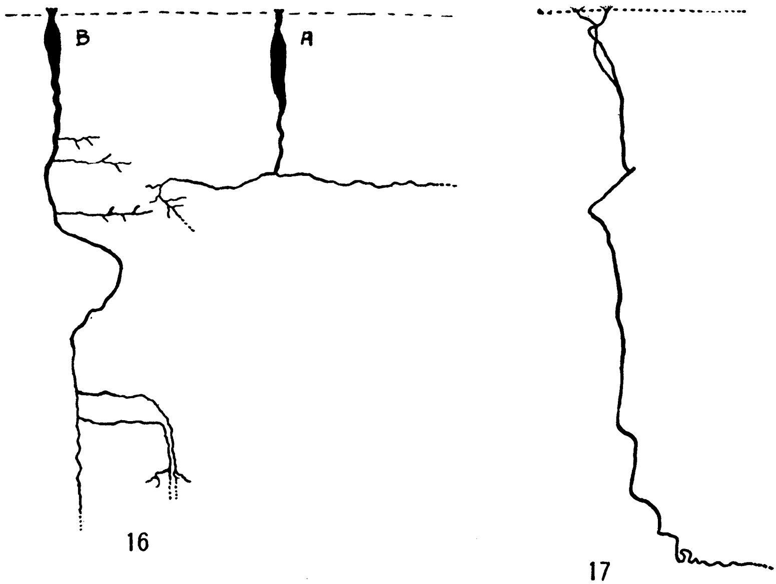



FIGS. 14, 15.—Fig. 14, vertical extension of root system of *Euphorbia* sp.; fig. 15, vertical extension of root system of *Sphaeralcea cuspidata.*

SHRUBS

*Parosela formosa.*—This low, much branched shrub is confined almost entirely to the sides of arroyo beds in the *Fallugia* association. The leaves are very small and xerophytic in structure. Several root systems were dug up and found to belong to the specialized type with prominent laterals, resembling somewhat the

cactus type. In some specimens no tap root could be distinguished, although a better development of the tap root was found in plants




FIGS. 16, 17.—Fig. 16, vertical extension of plants of *Berlandiera lyrata: A*, growing 1 ft. above arroyo bed; *B*, growing 4 ft. above arroyo bed; fig. 17, vertical extension of root system of *Gaura coccinea*.

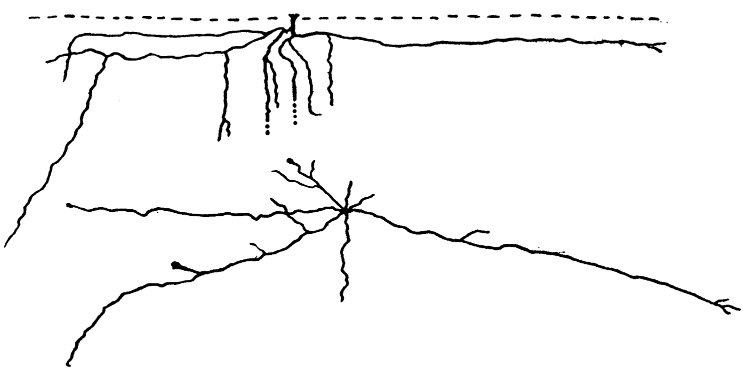


FIG. 18.—Vertical and horizontal extensions of root systems of *Parosela formosa*

growing higher above the arroyo bed. The plant shown in fig. 18 grew on the edge of a gravelly arroyo bed 6 ft. wide. The specimen

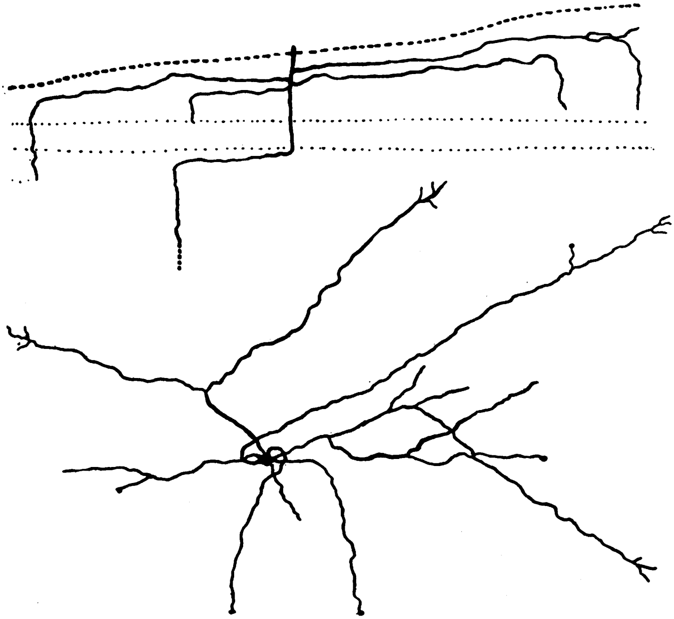


FIG. 19.—Vertical and horizontal extensions of root system of *Artemisia tridentata*

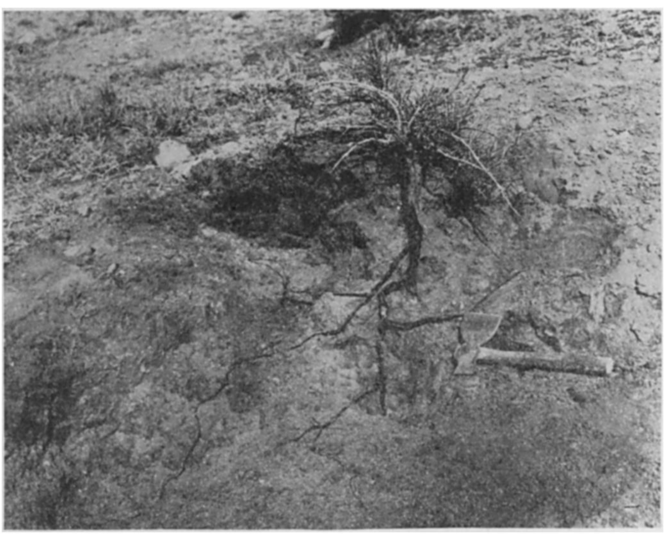


FIG. 20.—Root system of *Ephedra trifurca*

was 28 in. in height. The tap root was weak, being exceeded in diameter by several of the laterals. The laterals were numerous and arose just below the ground and proceeded horizontally 2 or 3 in. below the surface, most of them beneath the bed of the arroyo. The ends of several of them dipped abruptly downward. This type of root is rare in the region. The root system of *Parosela scoparia*, which grows in sand, was found to be similar, but more deeply placed.

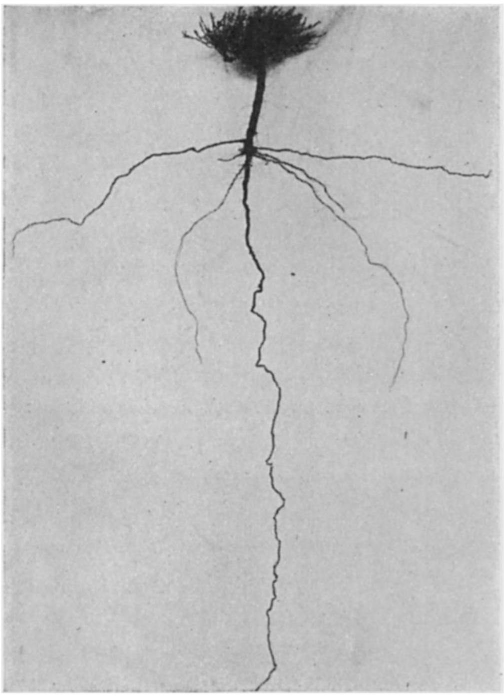


FIG. 21.—Root system of *Dysodia acerosum*

*Artemisia tridentata*.—This plant grows along the sides of arroyos in the *Chrysothamnus* association. Well developed specimens are rare, since the plant is freely eaten by grazing animals. The specimen shown in fig. 19 grew in soil the upper 10 in. of which was adobe, overlying 12 in. of coarse gravel and pebbles, with adobe below this to an unknown depth. The tap root was well developed, but the laterals near the surface were extremely prominent. These were of two types: numerous short ones in the upper 12 in. of soil, and a few very long ones which arose from the upper 6 in. of the tap root. The latter proceeded horizontally 3–4 in. below the surface of the soil and reached a length of 20–40 in. There was a tendency for the ends of these roots to turn downward, as in *Parosela*.

*Ephedra trifurca*.—This is one of the dominant species of the *Dysodia-Ephedra* association. Investigation of a number of

specimens showed a considerable variation in the root system, which in general has a good development of both tap and lateral roots. The plant shown in fig. 20 grew in adobe soil about 2 ft. above the bottom of an arroyo and had prominent laterals and a stout but rapidly tapering tap root. Below the part shown in the photograph, two large laterals were given off, below which the tap root was insignificant. Another specimen growing in adobe soil 10 ft. above the bottom of an arroyo and exposed by erosion showed a relatively much greater development of the tap root. Several laterals, the largest half an inch in diameter, were given off in the upper 2 ft. of soil. Three small laterals occurred 3 ft. below the surface. The tap root proceeded somewhat tortuously downward to a depth of at least 11 ft., a little below the level of the arroyo bed, where a large lateral arose. Below this the tap root had a diameter of 5 mm. and was not followed farther. A third specimen grew on a hill and was exposed by the removal of gravel. The plant grew in a soil composed of boulders up to 8 in. in diameter, the interstices of which were filled with sand. The root system was essentially similar to the second specimen described. The cause of the variation in the length of the tap root apparently is not the character of the soil,

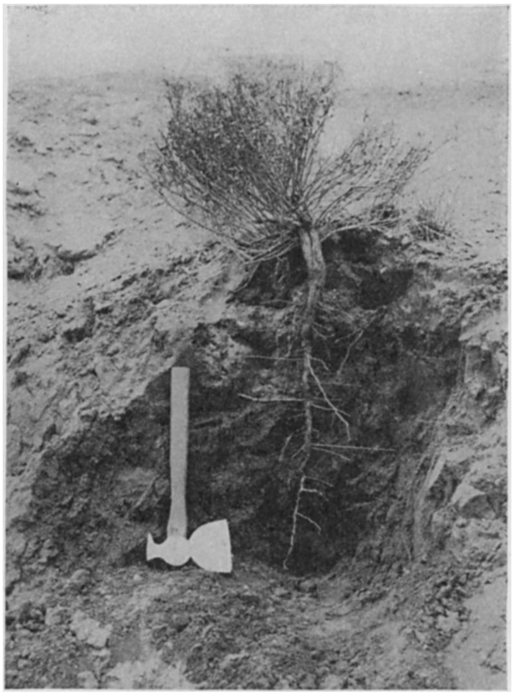


FIG. 22.—Root system of *Chrysothamnus Bigelovii*

but the height of the plant above the nearest arroyo. Even though there is a stream in the arroyo only a few hours each year, there is probably a layer of moister soil on a level with the bottom of the arroyo, on account of a slow creep of ground water toward the arroyo and the conservation of the moisture by the dry sand covering it.

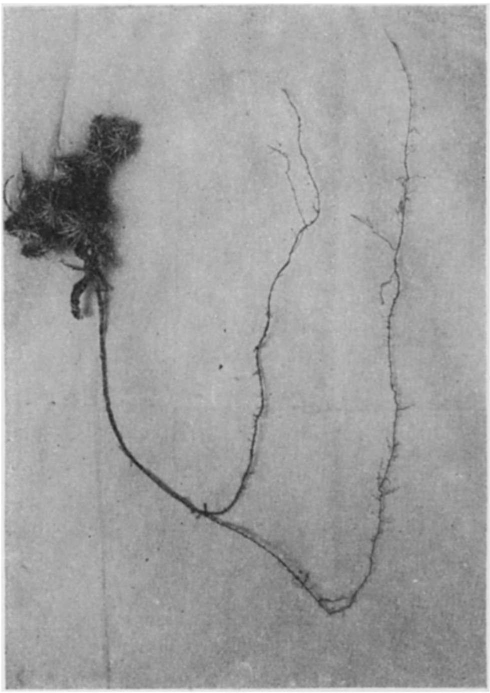


FIG. 23.—Root system of *Opuntia fragilis*

*Dysodia acerosum.*—The habitat of this plant is the same as that of *Ephedra*. The aerial parts of the plant form a compact, much-branched tuft. The leaves are needle-like. The individual photographed grew in sandy adobe with large pebbles (fig. 21). The plant had a stout tap root with a few large laterals arising close together a short distance below the surface of the soil. The tap root shown measures 39 in., but it was probably several inches longer. Both tap and lateral roots bore numerous fine branches. This species probably has the largest root system in proportion to the size of the aerial parts of any of the plants of the region.

*Chrysothamnus Bigelovii.*—This is the dominant plant in an association characteristic of the lower parts of the sides of arroyos. The principal photosynthetic work is done by the almost leafless green stems. The root system is of the generalized type. Fig. 22 shows only a part of the root system of a rather young plant. Later excavation showed laterals up to 90 and 100 in. in length and a tap root about 100 in. long. The laterals are usually of small diameter

and taper very slightly and bear numerous small lateral branches, especially near their distal ends. Older individuals probably have root systems more extensive than that of any other plant of the arroyos or mesa.

*Opuntia fragilis*.—This is the smallest and most common cactus of the mesa, where large colonies form mounds of sand or adobe. The root system is very superficial and consists of one or two main roots with numerous small lateral branches (fig. 23).

*Opuntia arborescens*.—This is the only large cactus found in the region. It is characteristic of the pine-cedar association of the mountains and occurs sparingly on the mesa. The specimen shown in figs. 24 and 25 grew in the latter situation and was only 2.5 ft. in height. The root system is similar to the type described by CANNON for the larger forms occurring near Tucson. There is a sharp differentiation of absorptive and anchorage roots. The former are long and thin and occur within an inch or two of the surface; the latter are short and thick and deeply placed. The longest absorptive root had a length of 93 in.; the longest anchorage root a length of 30 in. The absorptive roots have many fine branches, especially near the ends.

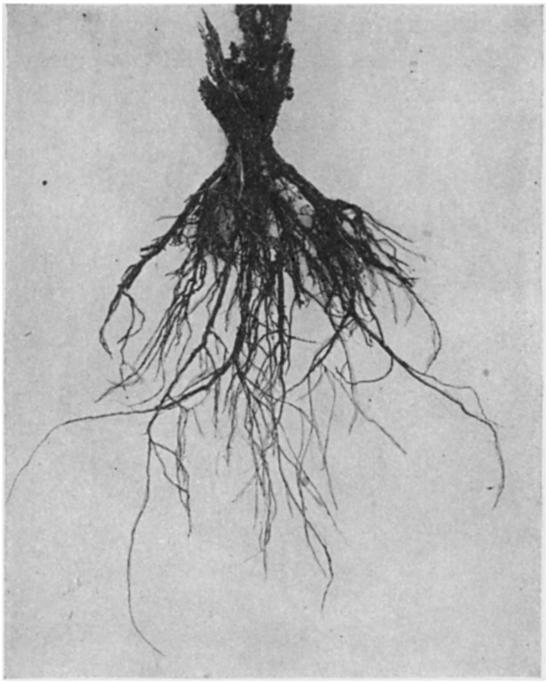


FIG. 24.—Anchorage roots of *Opuntia arborescens*, vertical extension.

*Opuntia camanchica.*—This is the common prickly pear of the mesa and arroyos. The specimen shown in fig. 26 occurred in the *Dysodia-Ephedra* association in gravelly sand with small boulders. The plant had been formed vegetatively from a fallen segment which had become buried. The roots had originated from the pulvini and the proximal 2 inches of each was tuberous. The root system conforms to the usual superficial type described by CANNON for the smaller cacti, except for the presence of one thick, deeply placed root. The plant is usually several joints in height, so that

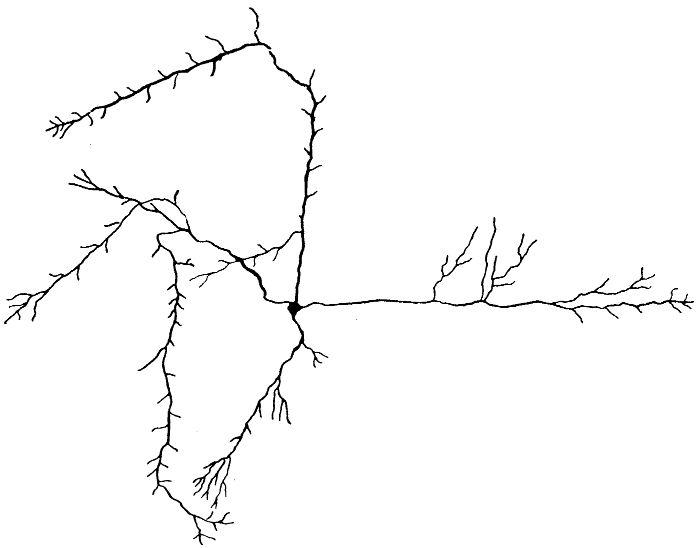


FIG. 25.—Absorptive roots of *Opuntia arborescens*, horizontal extension

especially in a strong wind there is considerable strain on the lower joint. The presence of the thicker, more deeply placed root may show a tendency toward the sharp differentiation of anchorage and absorptive roots so well shown by *Opuntia arborescens*.

*Mamillaria Grahami.*—This little cactus occurs sparingly in the driest parts of the *Dysodia-Ephedra* association. The root system differs from the usual cactus type in having a short but well marked tap root which bears many short and a few longer laterals.

*Yucca glauca.*—This plant is very common along arroyos on the mesa and in sandy soil. The plants generally grow in clumps

formed by vegetative multiplication. The root system consists of a thick, branched, horizontal portion bearing numerous laterals quite uniformly about 3 mm. in diameter. Those measured showed lengths of 5, 6, 7, and 24 in. The main root is usually about 2 in. in diameter and very succulent. It evidently functions as a storage organ.

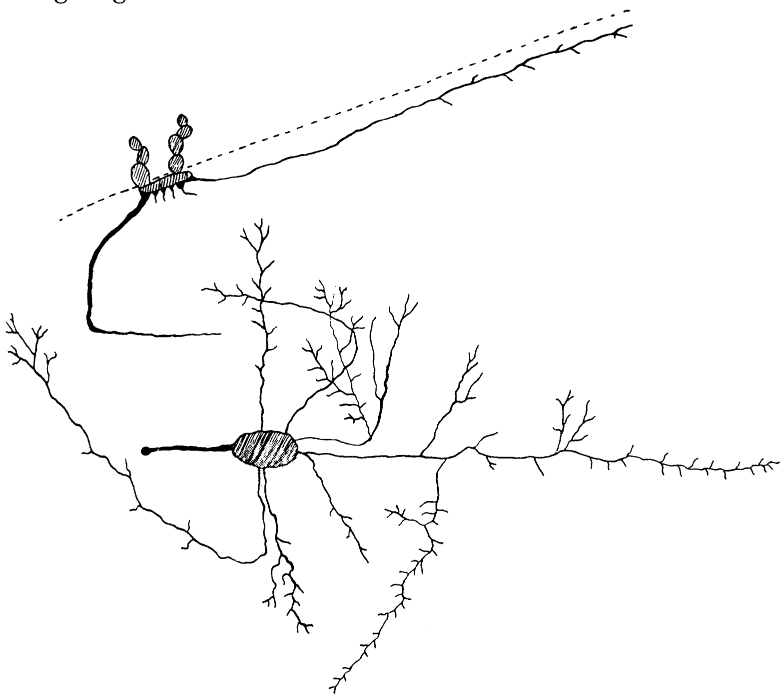


FIG. 26.—Vertical and horizontal extensions of root system of *Opuntia camanchica*

*Eriogonum effusum.*—This low shrub is characteristic of the edges of arroyo beds. The root system is of the generalized type. The plant shown in fig. 28 grew about 4 ft. above the bottom of an arroyo. The composition of the soil was as follows: upper 32 in., coarse sand and gravel; 10 in. of moist sand; dry gravel to an unknown depth. Several prominent laterals penetrated the sand and gravel layer. Two of the largest laterals occurred in the layer of moist sand. Another specimen, which grew about 10 ft. above the bed of an arroyo, had a tap root 80 in. long with the laterals

confined almost entirely to the space between the 16 and 24 in. depths. The effect of the position of the plant with reference to the arroyo bed is shown here.

*Gutierrezia Sarothrae*.—This semi-evergreen shrub is a common ruderal in many associations of mesa, mountain, and valley, but especially on the mesa, where grazing has been a greater disturbing factor. The plant shown in the photograph grew near the bottom of an arroyo and had a root system of the generalized type. The

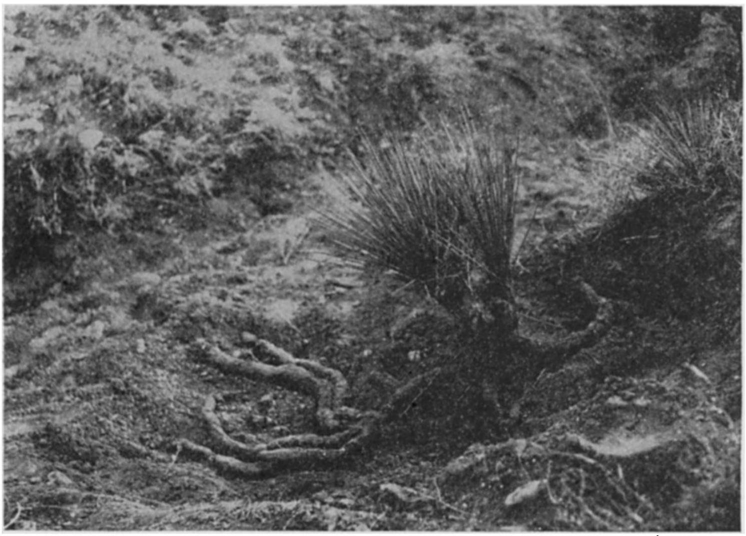


FIG. 27.—*Yucca glauca*

plant shown in the diagrams was a small specimen 8 in. in height and grew near the edge of the steep bank of an arroyo bed. The tap root was especially well developed and extended vertically to a depth of 44 in., where it reached the level of the bottom of the arroyo. Here the tap root turned and extended out under the bed of the arroyo a distance of 100 in., branching freely. The horizontal part of the root was within 2 in. of the surface and bore numerous fine absorptive roots. It is evident that the unusual development of this root system is a response to moisture conditions, and it is doubtless to this ability to respond to varying conditions that

the plant owes its success as a ruderal in so many associations (figs. 29, 30).

*Atriplex canescens.*—This evergreen shrub is common on the fans at the mouths of arroyos and less so along the sides of the smaller arroyos. A small plant 18 in. in height and growing in a small arroyo was selected for excavation. The upper 15 in. of the soil was sandy adobe, underlaid by 32 in. of coarse sand and gravel and 15 in. of hardpan. The plant had a strong tap root which forked at a depth of 32 in. One branch continued vertically downward and penetrated the hardpan layer. The other branch

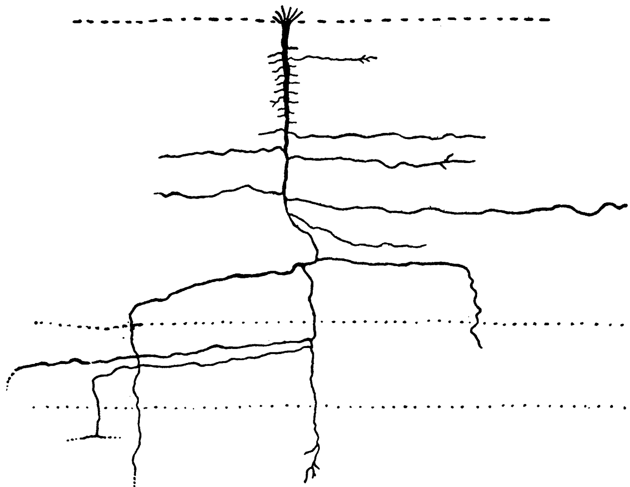


FIG. 28.—Vertical extension of root system of *Eriogonum effusum*

again forked and the subdivisions followed a tortuous course on top of the hardpan layer, twisting in every direction. One finally penetrated it diagonally. The effect of the hardpan in resisting root penetration was evident from the twisted character of the roots (figs. 31, 32, 33).

*Lycium pallidum.*—This solanaceous shrub is one of the most common plants along the sides of arroyos, especially where erosion is active. The root system is so peculiar that a large number of plants was examined. Unlike the roots of most of the plants of arroyo sides, the root system of *Lycium* is almost entirely horizontal.

A few laterals may extend upward. The main root of a specimen 18 in. in height was followed along the face of a steep bank for a distance of 15 ft., at which point the root was a quarter of an inch in diameter. The superficial character of the root system makes possible the vegetative multiplication by which the plant maintains itself in its unstable habitat. Erosion exposes the roots, which put forth new shoots.

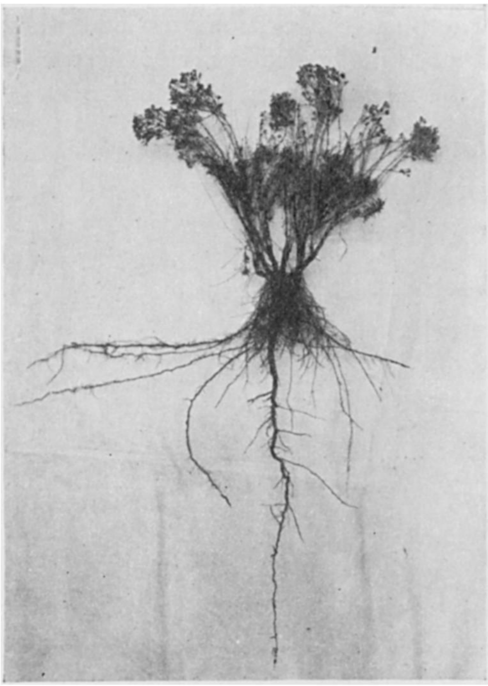


FIG. 29.—*Gutierrezia Sarothrae* from near bottom of arroyo.

## Discussion

On account of the fact that here, where the soil is of fluviatile origin, the conditions to which roots are exposed vary so much, even within the habitat of a single plant, the causes of any variations in the root systems are difficult to determine. Variations are common, but they may be due to one or more of a large number of soil factors, such as the composition of the soil, its penetrability, its alkalinity, its wilting coefficient, etc. The problem of the causes of root variation is one to be attacked under laboratory conditions, in which one factor can be varied at a time.

Observation, however, made apparent the effect of at least two factors, penetrability and water content. Roots were often seen to turn abruptly from a layer of clay or adobe and follow a thin layer of sand or fine gravel containing much less water but more easily penetrable. This is illustrated by the root system of *Solanum*

*eleagnifolium*, shown in fig. 11. A layer of soil difficult of penetration may cause much distortion of roots entering it, as seen in the diagram illustrating the roots of *Atriplex canescens*.

The most striking instance of the effect of a variation in the water content of the soil is shown in the roots of plants growing along arroyos. Nearly all of these are characterized by long tap roots, the length of which apparently is determined by the height of the base of the plant above the moister soil below the level of the

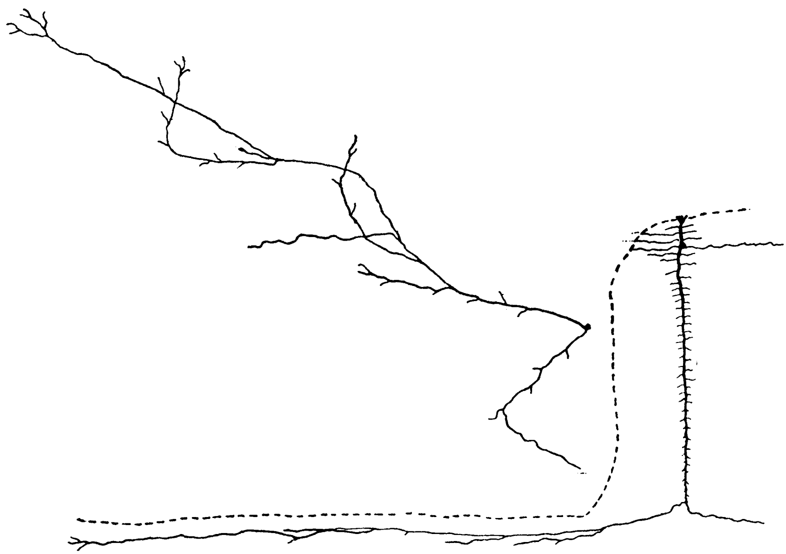


FIG. 30.—Vertical and horizontal extensions of root system of *Gutierrezia Sarothrae* from top of arroyo side.

arroyo bed. These variations are shown in the diagrams of the roots of *Ephedra*, *Gutierrezia*, *Berlandiera*, and others.

To which of the three general types of root systems that of a given individual belongs seems to be largely predetermined, a constant character of the species; but wide variations within the types, affecting the size and proportions of the root system, may occur through the influence of soil factors.

CANNON (*loc. cit.*) has pointed out the relation between the type of root system and the distribution of a species. In general, he finds that the species with root systems of the general type have

the widest distribution, while those with the specialized types are confined to peculiar habitats.

*Gutierrezia Sarothrae*, which has a generalized root system, is very widely distributed in primitive growths and as a ruderal. A number of species are confined here to the sides of arroyo beds and are characterized by prominent tap roots. *Lycium pallidum* has prominent horizontal roots and is confined almost entirely to rapidly eroding banks.

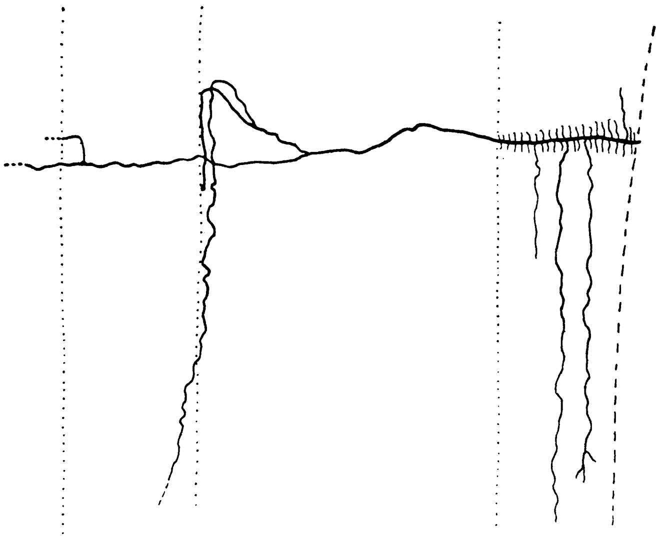


FIG. 31.—Vertical extension of root system of *Atriplex canescens*

Contrary to what might logically be expected, the species having the most fleshy roots grow in situations better watered than the average. *Cucurbita foetidissima* grows near irrigation ditches and along arroyos; *Rumex hymenosepalus* occurs in the broad arroyos crossing the mesa; *Berlandiera* is confined almost entirely to the sides of arroyo beds; *Yucca* occurs more commonly along arroyos than on the level mesa.

A knowledge of the interrelations of the roots of the plants of an association doubtless would throw light on many ecological questions. In a mesophytic association especially, the development of layers of the aerial parts of plants with reference to light

is very prominent. A comparable adjustment of the roots of plants with reference to soil moisture probably exists in all types of associations, but especially in arid habitats soil moisture is a limiting factor and root competition is more severe. Observations of the distribution of the roots of some of the associations were made on rapidly eroding arroyo banks and sand and gravel pits.

In the *Bouteloua* association, the most superficial layer of roots is that formed by the grasses, principal among which are *Bouteloua eriopoda* and *Hilaria Jamesii*. Most of the roots of these grasses occupy the upper 2 in. of soil, although some of them go much deeper. The roots of *Hilaria* are very tough and woody and reach a length of 6 ft. or more. The thorough permeation of the upper


32
33

FIGS. 32, 33.—Fig. 32, horizontal extension of root system of *Atriplex canescens* at depth of 44 in.; fig. 33, horizontal extension of superficial roots of *Atriplex canescens*.

layers of the soil by the roots of these grasses no doubt accounts for the relatively pure growth of grasses in this association. They so thoroughly remove the water from the superficial layer that seedlings of deeper rooted plants perish before the lower, moister layers are penetrated. Over large areas, overgrazing has destroyed most of the grass, giving opportunity for the entrance of such ruderals as *Gutierrezia* and *Salsola*.

In the *Dysodia-Ephedra* association, the upper layer of roots is made up of the roots of annuals, cacti, and grasses, such as *Bouteloua eriopoda*, *Hilaria Jamesii*, *Munroa squarrosa*, and *Pappophorum Wrightii*. These are very superficial and interfere little with the roots of the other plants of the association, as the grasses nowhere occupy large areas and the germination of seedlings is not prevented.

A second region of root penetration is occupied by the relatively superficial laterals so common among the plants of the region. These in general are more deeply placed than the roots of the grasses and annuals. *Dysodia acerosum*, *Aplopappus*, *Euphorbia*, and *Hymenopappus* are the principal plants.

A third layer of roots is made up of the lateral roots of *Ephedra* and the deeper parts of the root systems of *Dysodia*, *Allocarya Jamesii*, *Pachylophus hirsutus*, *Melampodium*, and others.

The fourth layer probably does not always occur, but near an arroyo it may contain more roots than any except the superficial layer. Here occur the ultimate branches of the tap root of *Ephedra*, *Gaura coccinea*, *Berlandiera lyrata*, *Stephanomeria runcinata*, and others.

The zonation of the roots reduces competition and permits the growth of a larger number of species. The root systems of the two dominant plants compete but little, since the principal absorptive roots of *Dysodia* occur in the third layer and those of *Ephedra* in the third and fourth layers. This no doubt accounts for the joint dominance of the two plants.

## Summary

The region at Albuquerque differs from that of Tucson in having about two-thirds as much rainfall and much lower winter temperatures. The soil of the mesa is fluviatile in origin and very diverse in composition. The hardpan layer prominent at Tucson is not well developed. The winter annuals and the larger shrubs and cacti are absent. Most of the plants are perennial herbs.

The root systems generally penetrate rather deeply, but often have prominent laterals near the surface of the soil. The cacti and a few of the shrubs have a very superficial root system. The larger cacti show a differentiation into anchorage and absorptive roots. The plants of arroyo sides have prominent tap roots varying in length with the height of the plant above the bottom of the arroyo. Storage roots are uncommon and are more characteristic of the moister situations. Vegetative reproduction from roots is common in the plants of unstable soil.

While the causes of root variation can be accurately determined only under laboratory conditions, two factors exert a very evident influence, variation in the penetrability of the soil and in its moisture content.

The roots of the plants of an association are grouped into rather definite layers, so that root competition is lessened. The composition of an association is probably determined largely by root competition.

The writer wishes to express his appreciation of the assistance of Professor Henry C. Cowles during the course of this investigation.

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